# The Tall-Fescue Endophyte

Evolution meets economics in the tale of the nation's most popular planted grass, which owes many of its qualities to a fungus toxic to livestock

Donald M. Ball, Jeffrey F. Pedersen and Garry D. Lacefield



Figure 1. Rural landscapes of the upper South get much of their lush green color from tall fescue, the most widely grown pasture and turf grass in the humid central and eastern United States. But tall fescue's reputation is mixed. The qualities that have made the cool-season perennial popular—its adaptability to various soils and difficult climate conditions and its resistance to insect and nematode attacks—derive largely from an internal fungus, or endophyte, that has



evolved with its host. Unfortunately the endophyte also has toxic and costly effects on grazing animals. (Painting by Judy Kitzman.)

motorist traveling the rural roads A of the upper South and lower Midwest is likely to get an eyeful of greenmuch of it a certain hue that a farmer might call "fescue green." Although Kentucky is known for its bluegrass pastures, in fact another grass dominates the abundant turf and pasture land throughout most of Kentucky and nearby states, especially those to its south, east and west. The European cool-season perennial known as tall fescue now occupies more acreage in the United States than any other introduced grass, giving the plant an enormous role in the nation's agricultural economy. But it has become clear that tall fescue, planted for its vigor, lush beauty, pest resistance and tolerance of drought and poor soils, is associated with a problem—perhaps as costly as a billion dollars a year—in the livestock industry. The effort to identify and eradicate the source of the problem is a story of importance both to science and to the nation's agricultural productivity.

Not long after tall fescue became popular in the late 1940s, farmers began noticing declining health and productivity among cattle, horses, sheep and dairy cows that grazed on the new forage. Despite the grass's high nutritional quality, beef-cattle producers talked of "fescue toxicity," which showed up as rough hair coats, intolerance to heat and poor weight gains among their animals. A gangrenous condition that sometimes develops on the extremities, especially the rear feet, during cold weather became known as "fescue foot." Bovine fat necrosis, the deposition of masses of fat in the abdomens of cattle, was observed among cattle grazing nearly pure stands of tall fescue that were highly fertilized with nitrogen.

Horse producers found that mares grazing tall fescue often abort, have foaling problems, give birth to weak foals and produce little or no milk. Weight gains among sheep showed the declines observed in beef cattle, and dairy animals often showed sharp depressions in milk production.

Although farmers had eagerly adopted tall fescue as a multipurpose grass, many livestock and dairy producers turned away from it once these problems were recognized. In many areas there were no other productive perennial pasture grasses, and so the need for a solution for the animal-toxicity problems associated with tall fescue was obvious.

In 1973, the crucial clue to the animal disorders was found at a farm near Mansfield, Georgia. The cattle in one tall-fescue pasture were exhibiting fescue-toxicity symptoms, but animals in a nearby pasture were not. J. R. Robbins, Charles W. Bacon and J. K. Porter, scientists at the U.S. Department of Agriculture's research station at Athens, began an investigation of this puzzling situation. Eventually they took samples from both pastures to test their hypothesis that a fungus might be at fault. In the laboratory they found strong support for their idea: Virtually all the grass in the pasture where the cattle were sick was infected with an internal fungus, or endophyte, whereas only about 10 percent of the grass in the other pasture was infected.

The identification of a culprit in the tall-fescue endophyte, whose role in livestock disorders was to be confirmed by many experiments that followed at many locations, was a breakthrough of remarkable importance. But like many research findings, it pointed the way to new questions. Could, and should, the fungus be eradicated, or at least controlled, or its toxic effects ameliorated, and how? Could pastures be kept endophyte-free? What is the mechanism by which a grass endophyte affects livestock health? How is endophyte infection maintained in the grass? What effect does the endophyte have on the grass itself?

The answers to these questions cross the boundaries that separate science, economics and agricultural practice. The endophyte turns out to be a splendidly adapted fungus that has coevolved with its host, to their mutual benefit. Its animal-toxicity effects are among several protective advantages the fungus provides to the grass, and are part of a complex plant-animal-fungus relationship that may actually be common among grasses and weeds.

Donald M. Ball is a professor of agronomy at Auburn University. He is a graduate of Auburn University, where he received a Ph.D. in 1976. He has specialized in forage crops since 1976 and has done agronomic consulting work in several states. Jeffrey F. Pedersen is a research geneticist with the U.S. Department of Agriculture's Agricultural Research Service and a professor of agronomy at the University of Nebraska, where he received his Ph. D. in 1981. Garry D. Lacefield is a professor of agronomy at the University of Kentucky and holds a Ph.D. from the University of Missouri (1974). Address for Ball: Department of Agronomy and Soils, Auburn University, AL 26849.



Figure 2. Kentucky 31, the vigorous tall-fescue variety responsible for the rapid adoption of tall fescue in the United States in the late 1940s and 1950s, was collected from this hillside in Menifee County, Kentucky, in 1931 by the late E. N. Fergus, a professor at the University of Kentucky. Fergus and his colleagues planted and evaluated the ecotype before the 1943 release of the new variety, now used widely for forage, turf and conservation. The seed was infected with the endophyte *Acremonium coenophialum*, which was implicated in animal toxicity in the mid-1970s. Because most tall fescue in the U.S. is of this variety, most is endophyte-infected.

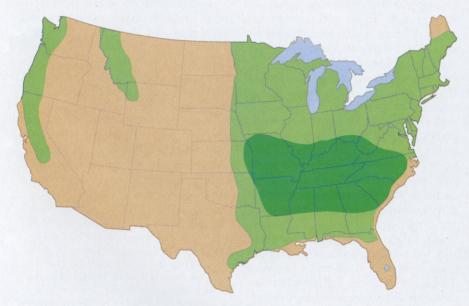


Figure 3. Range of tall fescue's adaptation (*light green*) includes most of the eastern U.S. and parts of the Pacific Northwest, but its area of primary use (*dark green*) is in the upper South and lower Midwest, where it is the dominant grass. In much of this area, climate and soil conditions are not suited to other grasses; thus tall fescue has been the overwhelmingly preferred grass for hay and livestock production. (Adapted from Buckner and Bush 1979.)

The forage producer's fight against it is, in a way, a small battle against the forces of evolution.

Tall Fescue and Its Endophyte

Now a popular introduced grass in many countries, tall fescue (Festuca arundinacea Schreber) was planted in the United States in the late 1800s, but it did not come into widespread use until well into the 20th century. In 1931, E. N. Fergus, a professor of agronomy at the University of Kentucky, visited the farm of William O. Suiter in Menifee County, Kentucky, where he found a particularly vigorous tall-fescue ecotype. The seed he collected and evaluated was released in 1943 as the cultivar Kentucky 31. It was widely adapted, had a long growing season, resisted pests and persisted under a wide range of conditions, including drought, poor soils and variable soil pH.

The new cultivar grew swiftly in popularity, becoming the grass of choice for forage, turf and soil conservation in the humid south-central states. Tall fescue, overwhelmingly dominated by the Kentucky 31 cultivar, is now grown on more than 35 million acres in the United States, on parks, playgrounds, athletic fields and lawns and along highways and waterways in addition to fields used for pasture and hay production.

But the reports of animal disorders sent agricultural scientists into the laboratories in the 1960s. Early chemical analysis showed that alkaloid compounds found in the grass might have effects on livestock, in the same way that the alkaloids produced by the ergot fungi of the *Claviceps* genus cause the similar, often severe disorder called ergotism when ergot-infected grain is ingested. Causal relationships were not clear, however, and the source of the alkaloids was not known.

When the endophyte was identified in the mid-1970s by microscopic analysis of the pith tissue of the infected Georgia pasture grass, the patterns of animal disorders began to be explained. At first the endophyte was identified as Sphacelia typhina, the asexual state of Epichloë typhina, a fungus found on many grasses and known as choke disease. But taxonomists later decided that the endophyte found in tall fescue is sufficiently distinct to deserve a new species name-Acremonium coenophialum (Morgan-Jones and Gams). Grazing studies by Carl Hoveland of Auburn University soon confirmed the

association of the fungus with fescue toxicity. More recent tests of samples from tall-fescue pastures throughout the U.S. have shown that over 90 percent have high levels of fungus infection. It is estimated that three-fourths of the tall fescue in the country is infected.

An endophyte grows within a plant, and the tall-fescue endophyte is a particularly elusive fungus. Because it is not visible externally, diagnosis in the field is not possible, and laboratory analysis is required to detect its presence. The fungus's mode of reproduction makes it more elusive. A. coenophialum does not disseminate spores that spread infection through the field; rather, it is transmitted by seed from one generation to the next. This mode of transmission might not have allowed the fungus to become so prevalent, had it not been for a mutualistic relationship that gives infected plants a competitive advantage. The fact that Kentucky 31 has been such a successful grass may stem in large part from the fact that the original seed almost certainly contained

the endophyte.

The simple life of A. coenophialum begins in the seed, where its mycelium—the fungus's vegetative stage, consisting of a mass of convoluted filaments, or hyphae—can be seen under the microscope (with the help of a stain) between the embryo and the starchy endosperm that is the embryo's food. The fungus can survive in stored seed for a year or so. Shortly after the seed germinates, mycelial filaments begin growing with the plant-moving through the intercellular space between both stem and leaf cells in the emerging shoot. After seven days, mycelia can be detected in practically all infected seedlings. In the maturing plant the endophyte becomes concentrated in the leaf sheaths (rather than the blades), but as reproduction approaches the hyphae begin moving upward between the rapidly elongating cells of the flower stem. Finally the fungus becomes concentrated in apical regions where flower heads are to form, and then in the flower heads themselves, where it penetrates the tissues of ovaries and ovules. The fungus has been detected only in the mycelial state, and its spores have not yet been detected in the field.

### A Symbiotic Relationship

The simple and efficient life cycle of the endophyte seems to put very little



Figure 4. Mycelium of the tall-fescue endophyte grows as the plant grows, extending through the intercellular space between plant cells. In this microscopic view of a tall-fescue tissue sample, the filaments of the fungus can be seen with the help of a blue stain. Because the fungus is internal and causes no visible symptoms in the grass, laboratory analysis is required to diagnose endophyte infection in tall fescue. (Except where noted, photographs courtesy of Donald M. Ball.)

stress on its host, from which it apparently derives nutrition by way of the intercellular fluid. The fungus does not penetrate or alter the cells of the host plant, and tests comparing the growth of infected and uninfected tall fescue indicate that infection confers a variety of favorable attributes to tall-fescue plants.

Various studies have shown that infected tall fescue, at least in some environments, has more-rapid germination rates. Infected seed produces more tillers and seedlings that are heavier and more likely to survive. Infected plants have been shown to be capable

of higher seed production. In greenhouse studies, infected tall fescue showed greater overall resistance to drought, and drought-stressed infected plants were more likely than their endophyte-free counterparts to to exhibit leaf roll—a response to drought that reduces the amount of exposed surface area, and thus the amount of water lost by the leaves. In field studies, infected plants lost less water to evaporation. In addition, plant-parasitic nematodes of several species have been shown to be present in greater numbers in the vicinity of the roots of uninfected tall fescue.

Several studies conducted in stressful environments have shown that established stands of uninfected tall fescue are more prone to decline under stress. Some producers who have planted commercially available tall fescue that is endophyte-free have often had difficulty establishing or maintaining stands of the grass.

In nature, unpalatability is a common protective mechanism for plants. In greenhouse studies several species of insects appear to prefer uninfected tall fescue; not coincidentally, they survive and reproduce better when consuming the uninfected grass. Grazing livestock and laboratory animals alike prefer uninfected tall fescue, and eat more of it.

mycelium enters rapidly elongating stem cells active mycelium in vegetative plant mycelium active mycelium infects grass invades seedling ovule starchy endosperm mycelium embryo in seed

Figure 5. Life cycle of the endophyte *Acremonium coenophialum* is simple and follows the growth and reproduction of the host plant, tall fescue or *Festuca arundinacea* Schreber. In tall-fescue seed, the endophyte can remain viable for about a year. When the seed germinates, the fungal mycelium begins to grow, extending into the young shoot by growing through the space between plant cells. In the vegetative plant, the mycelium is concentrated in the leaf sheaths, rather than the blades, but as reproduction approaches, its filaments grow into the flower stem and ultimately invade the plant's ovaries and ovules, where they become encapsulated in the seed. Spores have not been detected in tall-fescue fields, but some *Acremonium* fungi are known to reproduce asexually by spores. The tall-fescue endophyte is transmitted solely through the seed.

Thus the toxicity that accompanies endophyte infection can be seen as another protective advantage acquired during the coevolution of the grass and its endophyte. By selecting seed from vigorous plants, plant breeders and seed producers have taken advantage of the benefits conferred by the endophyte; they have also unwittingly selected for animal toxicity.

The evidence that the animal symptoms now associated with endophyte infection in tall fescue are caused by ergot alkaloids produced by the fungus is not yet conclusive, but the circumstantial evidence is strong. When J. K. Porter, one of the USDA scientists who associated the tall-fescue endophyte with livestock-toxicity problems, analyzed his laboratory cultures, he found that the endophyte does produce several ergot alkaloids. More recent analysis has shown that the tall-fescue endophyte produces members of a chemical subgroup, the peptide ergot alkaloids, that are more active biologically than most ergot alkaloids. Although the fungus does not grow into the leaf blades, the alkaloids are regularly detected there, indicating that they are translocated throughout the plant after they are synthesized by the fungus. Experiments have shown that the parent alkaloid of the peptide subgroup, ergotamine, produces symptoms in cattle and sheep similar to fescue toxicity. In rats the daughter compounds found in tall fescue have been shown to be two to four times more toxic than ergotamine. And in recent tests one of the peptide alkaloids, ergovaline, was shown to cause fescue-toxicity symptoms when fed to steers. (No alkaloids have been found, however, in meat or milk from fescue-fed animals; the compounds appear to be fully degraded by the animals.)

## Problems in the Pasture

In an infected tall-fescue pasture, a rise in temperature in the summer can have a strong and visible effect on cattle. Instead of grazing, the cattle spend an inordinate amount of their time seeking shade and water. Their body temperatures and respiration rates are high, they salivate excessively and they gain little weight. These striking effects are sometimes called "summer slump." The condition is costly for livestock producers.

Experiments in several states have shown that for each 10 percent increase in the endophyte infection rate, the dai-





Figure 6. Leaf roll is a mechanism by which grass can reduce its surface area during dry conditions and thus minimize the loss of water by evapotranspiration. In experimental plots, tall-fescue plants that are not endophyte-infected exhibit little leaf roll (*left*); because precious water is lost through the thinner, wider leaf blades, uninfected plants have trouble surviving the stress of drought. During drought, infected tall fescue (*right*) is more likely to exhibit leaf roll and to survive.

ly weight gain among young beef cattle feeding on tall fescue drops by about one-tenth of a pound. The effects are greatest when the ambient temperature exceeds 31 degrees Celsius, but studies have shown that the endophyte has an effect on livestock productivity at any temperature. Because the summer effects are far more visible, coolweather effects sometimes go unnoticed, and productivity losses are often greater than producers realize, especially in cooler climates.

In a number of recent studies, pregnancy rates, weight gains and milk production of cows and sheep, as well as the weaning weights of calves and lambs, have been lower on infected tall fescue. The reproduction of animals under nutritional stress is especially likely to be adversely affected.

Finally, the tall-fescue endophyte is now known to be a common cause of reproductive problems among mares. In a 1986 experiment at Auburn University, 22 pregnant thoroughbred, quarter-horse, Arabian and Morgan mares were fed either infected or non-infected tall-fescue pasture grass and hay during gestation, foaling and the immediate post-partum period. All but one of the mares eating the infected fescue had foaling problems, only three of 11 foals were born alive and only seven of the mares

survived. Furthermore, only one foal from this group survived beyond the first week. The 11 mares eating endophyte-free fescue had normal pregnancies; all mares and all foals survived. The normal rate of reproductive problems among mares grazing non-fescue forages has been estimated at 11.5 percent.

The economic impact of these effects is hard to estimate, but it is significant. The largest cost has been incurred by beef producers in the form of slower

weight gains and reduced numbers of calves. Losses associated with horse reproduction, with milk production among dairy animals and with the growth and reproduction of sheep and other grazing animals are somewhat less. Fescue foot and bovine fat necrosis have had an impact that has not been quantified. A conservative estimate places the total livestock-related losses nationwide related to tall fescue at between \$500 million and \$1 billion a year.



Figure 7. Maintaining stands of tall fescue is difficult in many areas without the advantages conferred by the endophyte. In an experiment in Americus, Georgia, plots of uninfected (*left*) and infected (*right*) plants from the then-experimental variety Georgia 5 were established side by side. Although the plants were genetically identical, the far greater stress tolerance of the endophyte-infected grass resulted in dramatic differences in the stands. (Photograph courtesy of Carl Hoveland, University of Georgia.)

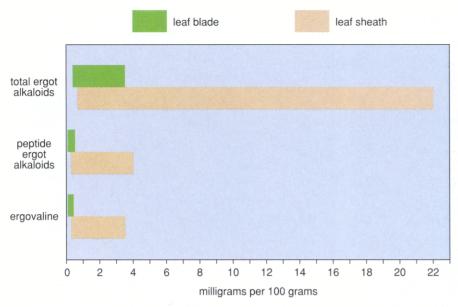


Figure 8. Ergot alkaloids are produced by the tall-fescue endophyte and can be detected in the leaf sheaths and leaf blades of infected grass, although the endophyte itself is found only in the sheath. Above are the ranges of some alkaloid concentrations detected in 15 samples of infected tall fescue collected from field and greenhouse. Ergot alkaloids are so called because they are produced by the ergot fungi (*Claviceps*) and are toxic to animals ingesting *Claviceps*-contaminated grain. They are believed responsible for the slow growth, reproductive problems and gangrenous disorders seen among animals grazing on endophyte-infected tall fescue. The most biologically active subgroup is the peptide ergot alkaloids, which are found in tall fescue; one of these compounds, ergovaline, has been shown to cause symptoms of fescue toxicity when fed to steers. (Data from Bacon et al. 1986.)

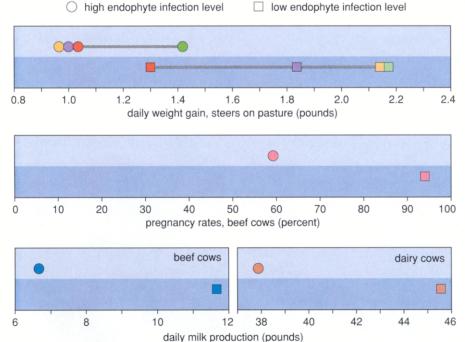


Figure 9. Animal performance is affected by the level of endophyte infection in tall-fescue pasture grass and hay. Experiments in numerous states have measured the average daily weight gain of beef steers in pastures that had low or high levels of endophyte infection, and consistently found that weight gains were significantly depressed by endophyte infections. Results from four grazing experiments, distinguished by color, are shown in the top panel. Beef cows grazing highly infected pastures are likely to have lower pregnancy rates (middle), and the daily milk production of both beef and dairy cows fed on tall fescue (bottom) is greatly reduced in the presence of endophyte infection. (Data from various studies, as reported in Stuedemann and Hoveland 1988; also Gay et al. 1988.)

#### **Planting Decisions**

The information emerging from research on the tall-fescue endophyte has presented livestock producers with a dilemma. If they graze animals on infected grass, performance will be less than optimum. If they attempt to establish and maintain a stand of endophyte-free tall fescue, they know it will be more difficult and expensive, and that the stand may be prone to fail under a stress such as drought. Other grasses are not well adapted in many areas, especially the warmer parts of the region, which is why tall fescue became so popular so quickly. Along the edges of the area of primary adaptation, higher levels of environmental stress are most likely to result in poor stands or stand losses if producers try to establish endophyte-free pastures.

Short-term considerations complicate the decision for an individual forage or livestock producer. If a pasture of infected grass is to be destroyed and replaced with a new grass, there are issues of cash flow, erosion hazards and sustaining the livestock during the period of re-establishment. Thus, a producer must balance a complicated set of risks and uncertainties when deciding whether to replant.

Producers who plant endophyte-free tall-fescue seed must expect to put far more effort into managing their stands. During the year that the new grass is established, for instance, grazing should be restricted so that the plants are grazed no closer than 3 inches from the ground. Prudence dictates that overgrazing of established stands of endophyte-free tall fescue also be avoided, especially when subsequent severe climatic stress is likely.

In states where tall fescue is grown, livestock producers now have ways of monitoring endophyte infection in their fields to help in making management decisions. Producers typically collect plant samples and take them to university or private laboratories, where an estimate is made of the prevalence of fungal infection of tall-fescue plants in the field. The level of infection tends to increase in a field over time, presumably because the infected plants tend to outcompete uninfected plants.

As endophyte infection increases, producers must consider re-establishing the stand to maintain animal productivity. But there are several ways to manage the problem in the interim, and awareness of the endophyte has



Figure 10. Visual comparisons of animals grazing uninfected tall fescue (*left*) and endophyte-infected grass (*right*) are striking. Symptoms of fescue toxicity in beef cattle, especially evident during hot weather, include rough hair coats, intolerance to heat and poor weight gains. During cold weather a gangrenous condition sometimes develops on the extremities of animals fed with infected tall fescue. Because symptoms are less visible during fall and spring and because most producers do not have the benefit of side-by-side comparisons, many underestimate their losses from endophyte infection. Annual livestock-related losses related to the endophyte have been conservatively estimated at \$500 million to \$1 billion.

changed the management of infected tall fescue in forage fields. Traditional agronomic-management practices tend to thicken stands and increase the proportion of infected tall fescue in the diet of animals, and thus exacerbate animal disorders. Some producers now adjust the timing and levels of fertilization to favor other volunteer or planted pasture species, encouraging a mixture of grasses to "dilute" the effect of the toxins on animals. And since it has been shown that the toxic effects of the endophyte may be less in a pasture that is heavily grazed, some producers now use higher stocking rates—a greater density of grazing animals—in pastures of infected tall fescue.

Since the endophyte is concentrated in the seedheads of the grass, grazing on seedheads is a particular concern. There is an additional reason to discourage such grazing: It has been shown that between 1 and 2 percent of the seed ingested can pass through an animal's body with both seed and endophyte remaining viable. Animals thus can spread infected seed from one area to another in the 48 hours or so after it is consumed; by this method the

endophyte can easily be transferred into a uninfected field by a grazing animal moving from one pasture to the next. Producers are therefore encouraged to use techniques that reduce the amount of seed eaten by livestock.

In conventional pasture management, plant species are often mixed to extend the grazing season or to reduce the need for nitrogen-containing fertilizer through the use of legumes that add nitrogen to the soil. Clovers and some other legumes provide nitrogen fixation and good nutritional value and have long been grown with tall fescue. It now appears that some of the good results achieved by these mixtures come about because the other crops reduce the concentrations of endophyte toxins in a grazing animal's body. Therefore, mixed plantings are another technique available to producers trying to minimize animal problems.

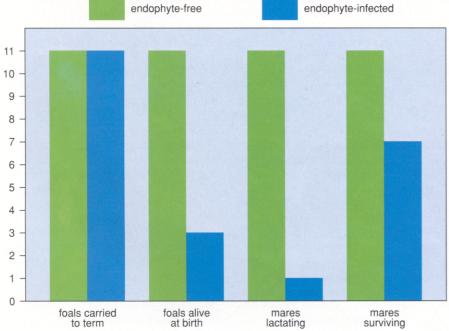
The question of mixed plantings is not, however, a simple one when the endophyte is involved. Legumes have vigorous seedlings and are easy to establish, and when planted with tall fescue—especially uninfected grass—they may initially compete so strongly that

they overwhelm the grass. But in an established stand, infected tall fescue tends to dominate. In addition to its sheer competitiveness, one interesting explanation could be allelopathy, the production by one plant of chemical compounds that suppress the growth of a competing plant. Recent studies have indicated that another Acremonium endophyte, found in perennial ryegrass, may have allelopathic effects on the establishment of legumes. Should the tallfescue endophyte turn out to have similar effects, it might help explain the difficulty livestock producers have had in maintaining forage legumes with infected tall fescue.

A final ecological issue in planting decisions is the possible effect of the tall-fescue endophyte on other organisms. The list of herbivores affected by endophyte-produced toxins may extend beyond insects and large mammals. The reproduction of rats and mice (in addition to several insect species) has been shown to be adversely affected by feeding on infected tall fescue.

The advantages of the endophyte to the grass continue to make endophyteinfected seed a popular choice for turf





uses. Seed producers now find themselves serving one or both segments of a split market, producing uninfected seed for livestock producers and infected seed for turf and conservation uses.

For most markets, seed marketers now must test tall-fescue seed for the endophyte, a matter of some inconvenience and expense. Many are opposed to requirements that seed tags state the proportion of infected seed in a quantity offered for sale, but a strong argument can be made that this is in the best interest of consumers. Such requirements are in effect in a few states, and there have been proposals to implement a federal seed-labeling requirement.

Additional issues now surround the production and marketing of tall-fescue seed. Since the endophyte loses its viability during prolonged storage, companies marketing seed for turf purposes have begun to test for and monitor endophyte levels and to consider special handling to ensure endophyte viability.

The discovery of the endophyte's role also has called into question much of what was believed to be established knowledge about tall fescue. Forage and livestock data from tall-fescue experiments prior to the early 1980s must now be considered suspect. It can be assumed that most early experimental tall-fescue pastures were infected, but the level of infection and the impact of the endophyte on experimental results cannot be known. Studies that had been thought to have established important facts about tall fescue may need to be repeated using seed whose infection status is known.

#### **Implications**

The implications of the tall-fescue endophyte story for agricultural science, and biological science in general, are broad and fascinating. It is now

Figure 11. Reproductive problems are common among mares that feed on infected tall fescue. In a study by scientists at Auburn University, the results of pregnancies among mares grazing infected and uninfected fescue were compared. The 11 mares fed endophytefree grass had successful pregnancies, but 11 mares in an infected pasture failed to lactate, and most produced stillborn foals during difficult deliveries. The foaling problems proved fatal to four of the mares. Shown at top are a healthy mare and foal in an Alabama tall-fescue pasture. Among livestock, horses are most affected by the reproductive problems associated with the tall-fescue endophyte. (Data from Putnam et al. 1990.)



Figure 12. Planting clover and other legumes with infected tall fescue, the approach used in this Alabama pasture, can greatly reduce the toxic effects of the tall-fescue endophyte. Establishing a mixed pasture can be difficult. Infected tall fescue competes strongly with legumes and is more persistent. In addition, an *Acremonium* endophyte in perennial ryegrass has been found to produce allelopathic compounds (compounds that suppress the growth of companion plants) that discourage the establishment of clover seedlings. It is possible that the endophyte of tall fescue may also have an allelopathic effect on clover. Prospects for reducing the impact of the endophyte on livestock production focus on techniques for using companion species with tall fescue, the development of more vigorous varieties of infection-free tall fescue, treatments to offset the effects of the endophyte and the genetic engineering of the fungus to reduce the production of toxic compounds while keeping the other advantages it confers on its host.

known that many species of grass, both wild and cultivated, contain endophytes. Undoubtedly many of these also have coevolved with their hosts; they may have played a large role in determining the ecological significance of the host grass and its evolutionary relationships with animals and many other organisms. Because tall fescue is a species of great economic importance, it has been the subject of extensive experimentation. But the effects of endophytes in other grasses on livestock performance, plant persistence and ecological interactions are largely unknown.

Research in this area has the potential for a significant impact on animal performance and the profitability of the livestock industry. Genetic studies of *Acremonium* might, for instance, lead to the identification or the development, possibly by genetic engineering, of strains that confer great benefits on tall fescue but that are not toxic to eco-

nomically important animals. Plant breeders may be able to develop uninfected tall-fescue varieties that are more stress-tolerant, and veterinary scientists might be able to find treatments to offset the effects of grazing on infected tall fescue. Agricultural scientists are challenged to find ways to kill the fungus in existing plants without having to destroy and then re-establish stands, and to develop management techniques that minimize the toxic effects of the endophyte.

Meanwhile many producers face substantial losses, because their only option in the face of endophyte-induced livestock problems may be to turn to forage grasses without the stress tolerance and low management demands they have come to expect. The discovery of the endophyte has been one of the most interesting and important developments in the history of agricultural research, but much work remains to be done.

## **Bibliography**

- Bacon, C. W., J. K. Porter, J. D. Robbins and E. S. Luttrell. 1977. Epichloe typhina from toxic tall fescue grasses. Applied and Environmental Microbiology 34:576.
- Bacon, C. W., P. C. Lyons, J. K. Porter and J. D. Robbins. 1986. Ergot toxicity from endophyte-infected grasses: A review. Agronomy Journal 78:106–116.
- Ball, D. M., C. S. Hoveland and G. D. Lacefield. 1991. *Southern Forages*. Atlanta, GA: The Potash and Phosphate Institute and the Foundation for Agronomic Research.
- Buckner, R. C., and L. P. Bush, eds. 1979. *Tall Fescue*. Madison, WI: American Society of Agronomy.
- Fribourg, Henry A., C.S. Hoveland and Pascal Codron. 1991. Tall fescue and *Acremonium coenophialum*—review of current situation in the United States. *Fourrages* 126:209–223.
- Gay, N., J. A. Boling, R. Dew and D. E. Miksch. 1988. Effects of endophyte-infected tall fescue on beef cow-calf performance. Applied Agricultural Research 3:182.
- Hoveland, C. S., R. L. Haaland, C. C. King, Jr., W. B. Anthony, E. M. Clark, J. A. McGuire, L. A. Smith, H. W. Grimes and J. L. Holliman. 1980. Association of *Epichloe typhina* fungus and steer performance on tall fescue pasture. *Agronomy Journal* 72:1064–1065.
- Joost, R., and S. Quisenberry, Eds. 1993. Acremonium/Grass Interactions. Vol. 44 in Agriculture, Ecosystems and Environment. Elsevier: Amsterdam.
- Morgan-Jones, G., and W. Gams. 1982. An endophyte of *Festuca arundinacea* and the anamorph of *Epichloe typhina*, new taxa in one of two sections of *Acremonium*. *Mycotaxon* 15:311.
- Pedersen, J. F., G. D. Lacefield and D. M. Ball. 1990. A review of the agronomic characteristics of endophyte-free and endophyte-infected tall fescue. *Applied Agricultural Re*search 5:188–194.
- Pedersen, J. F., and D. A. Sleper. 1988. Considerations in breeding endophyte-free tall fescue forage cultivars. *Journal of Production Agriculture* 1:127–132.
- Putnam, M. R., D. I. Bransby, J. Schumacher, T. R. Boosinger, L. Bush, R. A. Shelby, J. T. Vaughan, D. M. Ball and J. P. Brendemuehl. 1990. The effects of the fungal endophyte Acremonium coenophialum in fescue on pregnant mares and foal viability. American Journal of Veterinary Research 52:2071.
- Read, J. C., and B. J. Camp. 1986. The effect of the fungal endophyte *Acremonium coenophialum* in tall fescue on animal performance, toxicity, and stand maintenance. *Agronomy Journal* 80:811–814.
- Rice, J. S., B. W. Pinkerton, W. C. Stringer and D. J. Undersander. 1990. Seed production in tall fescue as affected by fungal endophyte. *Crop Science* 30:1303–1305.
- Siegal, M. R., G. C. Latch and M. C. Johnson. 1985. *Acremonium* fungal endophytes of tall fescue and perennial ryegrass: significance and control. *Plant Disease* 69:179–193.
- Stuedemann, J. A., and C. S. Hoveland. 1988. Fescue endophyte: History and impact on animal agriculture. *Journal of Production Agriculture* 1:39–44.